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Roberts Creek Study Forest

Habitat Use of a Dispersed Retention Area by Breeding Winter Wrens

By
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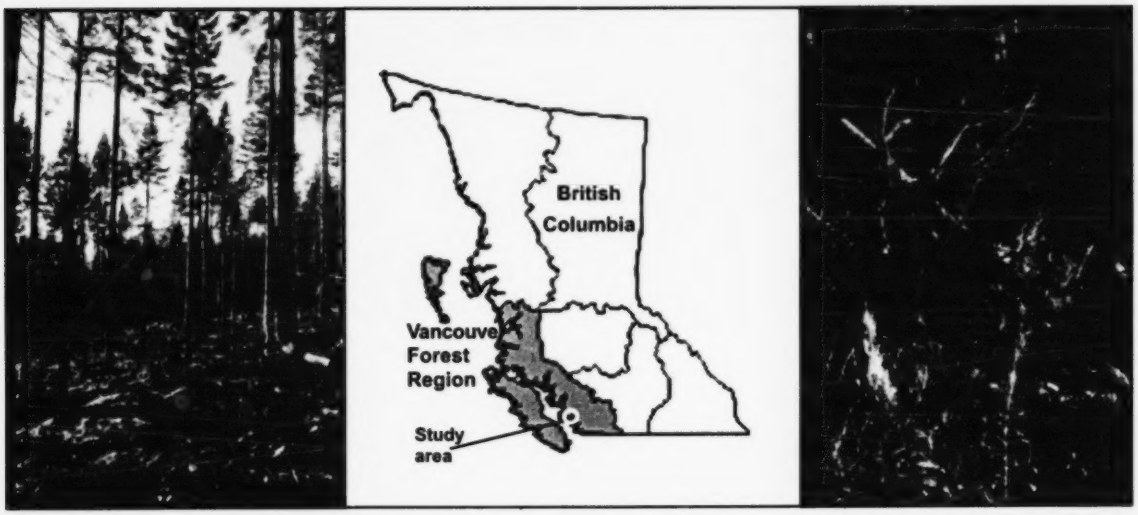

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Cover photos: At left, dispersed retention area in the Roberts Creek Study Forest, British Columbia, circa 1996. At right, Winter Wren nest in center of root wad, in the dispersed retention area, 1995.

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SUMMARY

The Winter Wren (*Troglodytes troglodytes pacificus*) is a common bird in British Columbia and is typically associated with pockets of complex forest structure. From 1995 to 1997, on the south coast of British Columbia, we studied Winter Wrens' use of habitat in a 13.1-ha pilot study block of mature (>120 years) forest. In the central area of the block, 7.1-ha had been harvested in 1993 to produce a uniform dispersed retention of single dominant Douglas-fir and western redcedar trees. We chose to study the Winter Wren because it is distributed throughout forests of the Pacific Northwest, and its habitat use and life history traits are sensitive to forestry practices. We focused on territorial and nesting behaviour of male wrens. Our results indicate that during the immediate post-harvest years, habitat quality of the dispersed retention area may be sub-optimal for breeding males because of changes to forest structure and amounts of habitat attributes. As well, habitat quality for Winter Wrens depends on site tenacity, annual weather, and proximity of structurally complex, closed canopy forest. Furthermore, we suggest streams and seeps may provide higher quality sites for nesting and foraging in either dispersed retention or mature forest despite their overall differences in stand structure. Based on these findings, we think that the overall effect of the dispersed retention system on wildlife will depend on the size of the block and its juxtaposition to other forest types. Understanding how forest practices affect a species, such as the Winter Wren, helps managers design forest practices that can provide habitat to wrens and other forest dwelling organisms which rely on similar structures and ecological processes.

KEYWORDS

Winter Wren, *Troglodytes troglodytes pacificus*, wildlife habitat, dispersed retention, forest structure, forest management planning, Vancouver Forest Region, British Columbia

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INTRODUCTION

In many areas of coastal British Columbia, retention of trees within cutblocks is becoming a common forest-management practice to help achieve wildlife habitat objectives, yet few studies have assessed the value of these retention systems for wildlife (Steventon et al. 1998; Beese and Bryant 1999; Sullivan and Sullivan 2001). Dispersed retention systems, for example, retain low densities of live pre-harvest trees distributed across the stand (Mitchell and Beese 2002). In part, dispersed retention is intended to maintain some stand-level and landscape-level habitat diversity by retaining forest stand attributes for habitat and by providing greater structural complexity than clearcutting (Keenan and Kimmins 1993; Franklin et al. 1997). The structural complexity of a forest is defined as a function of composition of overstory and understory tree species and vegetation, age and density of trees (dead and live), and environmental factors (Zenner 2000). Wildlife species that rely on forest stand attributes and on the structural complexity associated with mature or older forests may benefit from retention systems if retention systems lead to particular stand attributes and forest structure being achieved sooner or maintained longer over the rotation (Franklin et al. 1997).

To understand how the application of a dispersed retention treatment might change the availability of habitat, e.g., forest structure, or the ecological processes that produce habitat for wildlife, from 1995 to 1997 we conducted a pilot study of a common bird—the Winter Wren (*Troglodytes troglodytes pacificus*). We examined whether territorial and nesting behaviour of the wren changed as a result of the changes in quantity and distribution of habitat attributes. We selected the Winter Wren because of its broad distribution throughout forests of the Pacific Northwest and the Northern Hemisphere (Campbell et al. 1997), the lower cost for obtaining a large sample, and its habitat use and life history traits, which are sensitive to forestry practices.

Research on bird communities suggests that, in terms of habitat use and behaviour, the response of Winter Wrens to a harvesting regime may change with the type of regime. Winter Wrens can be found in a variety of forest stands, but they are lower in density or absent from clearcuts (Chambers et al. 1999; Savard et al. in press). Their territories are associated with complex forest structure and often include riparian areas (McGarigal and McComb 1992; Waterhouse et al. 2002) and disturbed sites (Wesolowski 1983). Winter Wrens may be sensitive to forest fragmentation, preferring interior habitats of mature or old-growth forests (Hansen et al. 1993; McGarigal and McComb 1995). Foraging and nesting behaviours of the Winter Wren might vary according to the type of harvesting regime and silvicultural system because wrens are insectivores that are, in turn, preyed upon by species such as Douglas' squirrels (*Tamiasciurus douglasii*) (pers. observ.), hawks (*Accipiter* sp.) (pers. observ.), and marten (*Martes americana*) (Nagorsen et al. 1989) that are also sensitive to forestry practices. As well, males defend small territories (usually <2.0 ha) in which they weave nests in cavities or behind bark of snags and logs, in cavities in root wads and stream banks, or among tree branches (Wesolowski 1983; Waterhouse et al. 2002). Males can be polygynous and females can have more than one brood; hence, territories often contain several nests built by the male from which the female(s) choose(s) one for breeding (Armstrong 1956; Waterhouse et al. 2002). High-quality habitats may support more nests than do low-quality habitats (Armstrong 1956; Armstrong and Whitehouse 1977).

STUDY OBJECTIVES

The dispersed retention area was harvested as a pilot block in 1993 in the mature (80–>120 years) Roberts Creek Study Forest (D'Anjou 2001b).[1] A replicated silvicultural systems installation was intended to follow the pilot block in the Study Forest. We planned to use the findings about the use of habitat by Winter Wrens, from this study and a study in the unmanaged mature forest (Waterhouse 1998; Waterhouse et al. 2002), to guide further research of how different silvicultural systems affect habitat values. Instead, however, in 1997 a series of unreplicated adaptive management case studies were installed to demonstrate and monitor different silvicultural systems (D'Anjou 2001a). Hence, we did not continue the Winter Wren project and this technical report summarises our research findings from the pilot block. Our objectives are to:

1. describe habitat use of breeding Winter Wrens in a block harvested according to a dispersed retention system; and

2. compare these findings with those on habitat use in young and mature forests.

DESCRIPTION OF STUDY FOREST AND STUDY BLOCK

The Roberts Creek Study Forest is on the Sunshine Coast, approximately 40 km northwest of Vancouver, British Columbia (*see* front cover). It is a mature forest of wildfire origin with a tree species composition typical of the Coastal Western Hemlock drier maritime variant—i.e., dominated by Douglas-fir (*Pseudotsuga menziesii*) with western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) in lower crown classes (D'Anjou 2001a, b). Pre-fire veteran Douglas-fir trees and snags, and redcedar snags, remain throughout the forest, although post-fire harvesting activities focused on extraction of redcedar snags for shakes and shingles (D'Anjou 2001a). Summers are relatively dry and warm in this vari-

[1] The second pass occurred in 1999.

ant, while winters are moist and mild with low snowfall (Meidinger and Pojar 1991).

We surveyed 13.1 ha, of which 7.1 ha (54%) had been harvested as a dispersed retention block in 1993. Unlike other studies within the same dispersed retention area (D'Anjou 2001a; Hudson and D'Anjou 2001), our study block included mature forest extending approximately 150 m beyond the boundaries of the dispersed retention block, except on the northern boundary, which is a logging road. Small streams (average channel width ≤3 m) flow through the mature forest on the eastern and western edges of the dispersed retention area, and an intermittent stream (zero-order, ephemeral) flows through the eastern portion of the dispersed retention area (*see* Figure 1) (Hudson and D'Anjou 2001).

In the first harvest entry during the fall of 1993, trees were handfelled and then yarded by a cable system. The retained trees were mostly dominant Douglas-fir (average 65 cm dbh) and some western redcedar, left singly in a relatively uniform pattern. Approximately 57 stems/ha (10%) of the pre-harvest trees and 249 m^3/ha (27%) of the pre-harvest volume remained standing but this increases to 68 stems/ha when including the trees buffering the streams (D'Anjou 2001a). During the 1993 winter, 25% (15 stems/ha) of the residual stand density was windthrown, after which about 53 stems/ha (6.3% of the pre-harvest stand density; 21.8% of the pre-harvest volume) remained standing. In 1994, Douglas-fir and western redcedar were planted in the spring and windthrown stems were salvaged by helicopter in the summer.

STUDY METHODS

Data Collection

From April to June in 1995 and in 1996, male Winter Wrens were captured in mist nets[2] (Falls 1981) then banded[3] for identification. We recorded sex[4], age class[5], weight (g), and left wing chord (mm) of each captured individual. Simultaneous with banding, we conducted surveys and mapped territories of males by recording their observed behaviours (Bibby et al. 1992) on a 25-m square (slope-corrected) flagged grid that overlapped the study block. Surveys were systematically conducted within 50 m of each grid flag, two to three times per week, just after dawn for up to 5 hours. Observers walked different routes ensuring that coverage of the study block varied with time of surveys. In addition, each male's behaviour was recorded for >30 min each week, but we did not assess dominance of individuals. Behaviours that we used to infer territorial boundaries of males included conspicuous singing and counter-singing, aggressive encounters

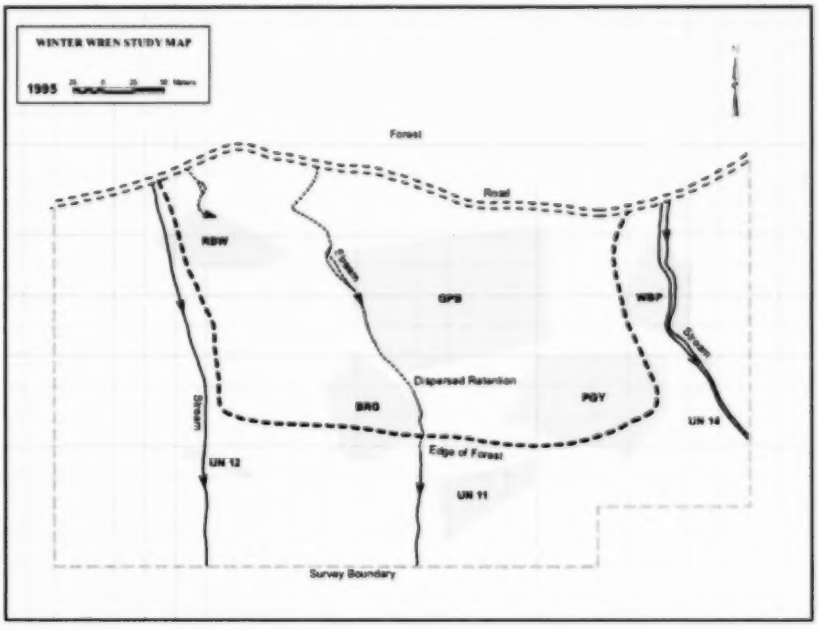

Figure 1. Distribution of territories for seven Winter Wrens in a 7.1-ha dispersed retention area and adjacent 6 ha of mature forest during 1995.

and agonistic counter-chipping between two males; nest locations; displays to attract females; and carrying of food for young. It is likely that our surveys did not fully delineate foraging areas, hence we consider territories to reflect primarily the core breeding area. We searched for nests in each territory by checking forest structures, in addition to using observations of displaying males, singing males, and adults carrying nesting material or food (Waterhouse 1998). Each nest was flagged and thereafter checked regularly from a distance ≥10 m (Waterhouse 1998). In 1997, although we conducted only five surveys in the study block, it was enough to obtain general locations of territories. We also undertook winter surveys three times during the study (November 1995, February–March 1996, and November 1996).

For habitat measurements, we included site characteristics and habitat attributes that provide security cover, escape cover, song perches, nest substrates, and foraging substrates for Winter Wrens (*see* Table 1). We measured habitat attributes in slope-corrected plots located every 50 m on the 25-m square grid, which produced a 50-m square grid of habitat plots (habitat grid) for the analyses. At plot centres, we measured site characteristics (slope and aspect) and horizontal distances to nearest water source and forest edge (Table 1). Ocular estimates of coverage of moss and vegetation <0.5 m high (herbs, shrubs, ferns, saplings) were taken in 2.65-m radius plots. Cover of vegetation >0.5 m high and tree canopy were estimated by canopy height classes, and trees and snags <10 cm dbh were estimated by canopy height classes measured in 5.64-m radius plots. Trees and snags ≥10 cm dbh were measured in 7.98-m radius plots. Percent cover of downed wood was estimated in 2.65-m radius plots for pieces ≤7 cm diameter, and in 5.65-m radius plots for pieces >7 cm diameter and aerial wood.

Data Analyses

First, we describe locations of territories and nests within the study block. Then, we use randomization tests to statistically examine by year whether wrens use habitat in a non-random pattern and, if so, determine which habitat attributes they select for their territories[6]

Table 1. Site characteristics and habitat attributes measured in habitat plots.

Variable	Description
Site characteristics	
Slope (%)	n.a.
Aspect (170-2600)	n.a.
Habitat attributes	
Duff (%)	Coverage on ground.
Moss (%)	Coverage on ground including upper surface of pieces of downed wood.
Aerial wood (%)	Coverage by portions of pieces ≥0.5 m above the ground.
Downed wood (%)	Diameter piece size classes (diameters of <2, 2-<7, ≥7 cm) of wood on ground.
Total vegetation cover (%)	<0.5 m high herbs, ferns, shrubs.
Ferns (%)	<0.5 or ≥0.5 m high.
Shrubs (%)	<0.5 or ≥0.5 m high evergreen, deciduous, berry.
Shrub/Fern (%)	<0.5 or ≥0.5 m high deciduous and berry shrubs and ferns.
Coniferous canopy (%)	Understory: 0.5-10 m, 0.50-1.99 m, 2.0-10.0 m high. Overstory: co-dominants; Intermediates entering lower overstory canopy; Suppressed below overstory canopy but >10 m high; and total >10 m high.
Treed canopy (%)	Deciduous and coniferous understory 2-10 m high; overstory >10 m high.
Trees (stems/ha)	dbh class cm: <10, 10-29, 30-49, 50-74, ≥75, ≥50, ≥30, ≥10, and total.
Snags (stems/ha)	dbh class cm: <10, 10-29, 30-49, 50-74, ≥75, ≥50, ≥30, ≥10, for total and by two decay-hardness classes: hard or soft.
Nearest water source (m)	Horizontal distance.
Nearest forest edge (m)	Horizontal distance.

[2] Mist nets: 30-mm mesh, 6-m long, 4-m high.
[3] Aluminium bands (supplied by Environment Canada), size 0 in 1995, and size 0a in 1996, were used with 2 or 3 coloured plastic bands of 2.3-mm inside diameter. Band combinations did not exceed 2 bands per leg.
[4] Adult males are distinguished by song, sexual display, and cloacal protuberance; females are distinguished by incubation or presence of a brood patch (Pyle et al. 1987).
[5] Hatching-year juveniles are defined by yellow/orange gape, down, or evidence of moult, whether or not they are members of a brood, and immature song of males used from June to October (Pyle et al. 1987).
[6] Randomization tests are non-parametric and therefore can accommodate data collected by non-random sampling (e.g., systematic sampling as with the habitat grid points) and data subject to spatial autocorrelation (i.e., adjacent plots, on the 50-m scale of the habitat grid, whether inside or outside territories, are more likely to represent similar habitat than plots far apart).

(Edgington 1995). For each year, we test each habitat attribute separately by generating 1000 replicates of random configurations of the territories on the habitat grid (Nemec 1997). Replicates are independent because the random placement of territories for one replicate does not influence the placement of territories of the next replicate. For each replicate, we retain the same number of territories but place each territory randomly on the habitat grid so that it overlaps at least one sampling plot but there is no overlap of territories. We also retain the observed size and shape of each territory during each random placement (Figures 2 and 3), although we use only the portion of each territory that overlaps the habitat grid to calculate the test statistic. Retaining territory size and shape during random placement limits the different configurations available during random placements, but we think territory size and shape reflect social dominance of individuals, which could influence habitat selectivity.

First, for a replicate, we calculate the mean amount of a habitat attribute within each territory using those sample plots on the habitat grid within the newly positioned boundaries of the territory. Next for the replicate, we calculate a grand mean from all the territory means. We then produce an empirical distribution of the grand means from the 1000 replicates and use it to assess the statistical significance of the observed grand mean obtained from field observations. We calculate the probability (P) in the upper tail as the proportion of grand mean values in the empirical distribution greater than or equal to the observed grand mean value (e.g., if 10 of the 1000 grand means were greater than or equal to the observed grand mean, then P=10/1000=0.01) and in the lower tail as the proportion less than the observed grand mean value. We reject the null hypothesis of no association between territory location and habitat attribute for $P \leq 0.10$.

We use two different randomization tests to incorporate how behaviour of territorial Winter Wrens may limit access of conspecifics to suitable habitat, thus reducing availability of habitat (Waterhouse 1998). First we apply the Ranhab1 test, described above. If the mean amount of an attribute for the observed configuration of territories differs significantly from that of the random configurations of territories, then we infer that Winter Wrens exhibit habitat selection and that their territories contain higher quality habitat than areas outside of their territories. If Ranhab1 is non-significant, we then test further using Ranhab2. For Ranhab2, we use the same assumptions as Ranhab1 but also retain the observed spatial configuration among territories to account for intraspecific competition (*see* Figures 2 and 3). Therefore Ranhab2 is more restrictive than Ranhab1 and uses only a sub-set of the random configurations of territories available with Ranhab1. We reason that intraspecific competition may limit access to higher quality habitat because the territory boundaries of counter-singing males are generally 20 m apart, thus gaps of undefended area that contain preferred habitat can occur between territories (Armstrong and Whitehouse 1977; Wesolowski 1983). We might not detect habitat selectivity using Ranhab1 if higher quality habitat is present but not available because of intraspecific competition. Therefore, if the mean amount of an attribute for the observed configuration of territories differs significantly from that of random configurations of territories using Ranhab2, then we infer that Winter Wrens exhibit habitat selection. In this case, we suggest also that although their territories contain higher quality habitat, additional high-quality habitats likely occur between the territories. For testing of the 1995 data, we use all territories because we had no evidence that these birds were unsuccessful breeders. For 1996, we use two runs of the random analysis; in the first we include all territories, but in the second we exclude UN 52 because he appears to be an unsuccessful breeder, and such birds may be subordinate and use low-quality habitats (Hilden 1965).

RESULTS

Territories

We recorded seven territorial males in the study block in 1995, but we banded only five of them. In 1996, we recorded six territorial males of which one had been banded in 1995, and we banded another two of the males. We detected five potential territories, all held by unbanded males, in 1997. During our three winter surveys over 1995 and 1996, we did not detect any of the banded wrens. Surveys during spring revealed that gaps of undefended area occurred between adjacent territories in all years (Figures 1, 2, and 3). For both 1995 and 1996, the density of Winter Wrens (0.38 and 0.46 territories/ha, respectively), the proportion of the study block area within territories, and territory sizes were within the ranges of those reported for the mature forest (*see* Waterhouse 1998).

Territories appear to have broadly similar locations for 1995–1997, although only one banded territory holder returned—between 1995 and 1996 (Figures 1 and 2). In both 1995 and 1996, four territories contained both dispersed retention and adjacent mature forest, and one territory was solely within the dispersed retention area (Figures 1 and 2). We did not detect a central territorial male (Figure 3) during 1997, but the other territories tended to overlap locations used in previous years, with three of them located solely in mature forest. The ratios of total forested area to total dispersed retention area for the whole study block were similar for 1995 and 1996 (Table 2). Territories in 1996, compared to 1995, appear to shift outwards to include more area of mature forest (Figures 1 and 2). But mean area of the territories (Table 2) did not differ significantly (Mann-Whitney test, P>0.10). Total area covered by territories was greater in 1996 than 1995, although we had delineated one more territory in 1995 compared to 1996 (Table 2).

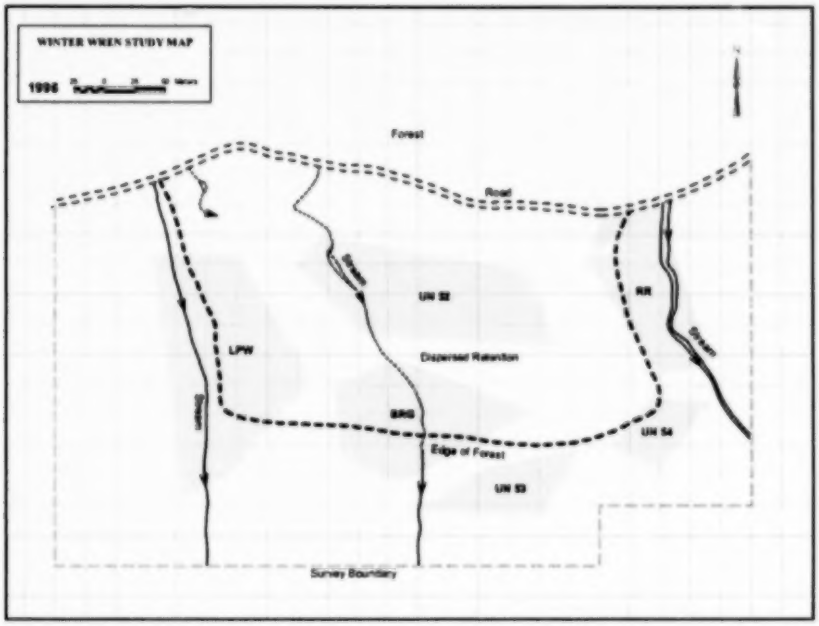

Figure 2. Distribution of territories for six Winter Wrens in a 7.1-ha dispersed retention area and adjacent 6 ha of mature forest during 1996.

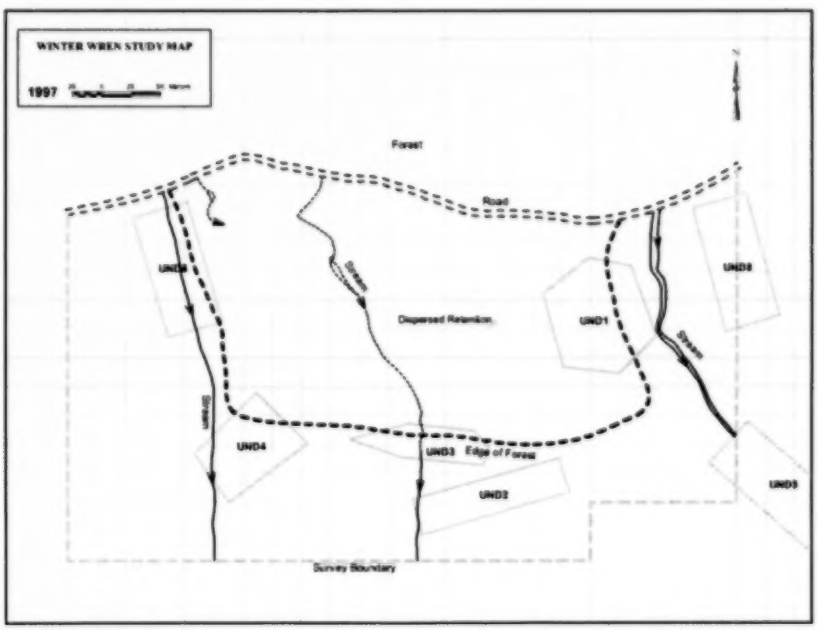

Figure 3. Distribution of territories for seven Winter Wrens in a 7.1-ha dispersed retention area and adjacent 6 ha of mature forest during 1997. Fewer data were collected in 1997, hence territory boundaries are only approximate.

Table 2. Description of territories and nests of Winter Wrens.

	1995	1996
Annual climate	Dry/mild	Wet/mild
Number of territories	7	6
Number of whole territories [a]	6	4
Mean area of whole territories (ha)	0.64 (0.21 SE)	1.12 (0.18 SE)
Range of size of whole territories (ha)	0.27-1.59	0.94-1.57
Area of study block within territories (ha)	3.86	5.09
Proportion of study block within territories (%)	29	39
Winter Wrens in study block [b] (no./ha)	0.46	0.38
Ratio of mature forest area: dispersed retention area in territories by year	0.73	0.70
Number of territories with nests (no.)	4	6
Total number of nests (no.)	6	9 [c]
Number of known active nests (no.)	6	4
Number of nests within mature forest (no.)	0	7
Number of nests within dispersed retention area (no.)	6	2 [c]

[a] Whole territories have complete boundaries within the study block, whereas partial territories extend beyond the study block boundaries.
[b] Partial territories contribute 0.5 of a territory as a standard unless <5% of a territory is in the study block in which case it contributes 0.
[c] Two of the nests identified in 1995 were re-lined in 1996, but both were inactive.

Nesting

During the 1995 and 1996 surveys, we located a total of 13 different nests (Table 2). Four of seven territories had a total of six nests in 1995, with two of these four territories having two nests each. Females used all six nests to hatch young. We found seven new nests in five territories in 1996. Two territories had two nests each, and three territories had single nests. Females used four of these nests, and they hatched young in four of the five territories. As well in 1996, within a sixth territory, the central territory in the dispersed retention area, two nests from 1995 (GPB, *see* Figure 1) were relined for use by the new territory holder (UN 52, *see* Figure 2). Yet UN 52, did not attract a female in 1996.

Nest substrates include root wads (n=3), logs (n=7, decayed at cavity, average piece size 45 cm, SE 7 cm), and snags (n=3, decayed at cavity, average dbh 22 cm, SE 8 cm). The distance of nests from streams and seeps averaged 11.0 m (SE 5.6 m) in 1995 and 6.7 m (SE 2.7 m) in 1996, but the two years did not differ significantly (Mann-Whitney test, $P>0.10$). All six nests found in 1995 were in the dispersed retention area, and the distance from the boundary with the adjacent forest averaged 35.6 m (SE 18.3 m). In 1996, the nests in the dispersed retention area were the two re-lined nests used by UN 52 (average 87.0 m from forest edge). One territory (UN 53) in 1996 had two nests within mature forest but this territory contained only mature forest. The five nests among the remaining four territories occurred in the mature forest, although the territories contained both dispersed retention and mature forest. For the seven nests located within the mature forest, the distance from the forest edge averaged 38.1 m (SE 6.0 m).

Randomization Tests

Winter Wrens placed their territories in a non-random fashion relative to several structural attributes of forests (Table 3). However, the significance of most of these attributes was not consistent between years. Furthermore, for 1996, we detected significant associations only after excluding UN 52. Nine of the 17 significant relationships were determined with Ranhab2. In general during 1995, Winter Wren territories, compared to those territories randomly placed, had fewer trees and hard snags in the largest diameter class (>75 cm dbh), although they had more trees in smaller diameter classes (10–29, 50–74 cm dbh) and more snags >10 m high (Table 3). Similarly, in 1996, lower densities of large snags (>75 cm dbh) and

Table 3. Attributes that characterize good-quality habitat of Winter Wren territories compared to that available based on randomization tests.

Year	Variable	Test [a,b]	Mean (SE) of attribute within territory	Mean (SE) of attribute outside territory	*P*-value
1995	Trees ≥75 cm dbh (no. stems/ha)	RN1	5.9 (5.9)	29.0 (7.2)	0.09
	Hard snags ≥75 cm dbh (no. stems/ha)	RN1	0.0 (0.0)	17.7 (6.4)	0.00
	Aerial wood (%)	RN2	1.2 (0.2)	2.3 (0.5)	0.08
	Trees 50-74 (no. stems/ha)	RN2	61.8 (24.8)	38.7 (11.0)	0.08
	Trees 10-29 (no. stems/ha)	RN2	105.9 (36.9)	98.4 (24.8)	0.06
	Snags >10 m high (no. stems/ha)	RN2	29.4 (14.9)	12.9 (5.2)	0.05
	Intermediate conifers ≥10 cm dbh (%)	RN2	5.3 (2.2)	4.1(1.6)	0.08
1996	Snags ≥75 cm dbh (no. stems/ha)	RN2	8.8 (4.8)	25.8 (7.3)	0.08
	Aerial wood (%)	RN1	1.0 (0.3)	2.4 (0.5)	0.10
	Downed wood <2 cm (%)	RN2	5.6 (1.0)	8.3 (1.2)	0.03
	Nearest water source (m)	RN2	33.7 (6.5)	55.4 (6.5)	0.04
	Nearest forest edge (m)	RN1	27.9 (3.2)	51.8 (5.5)	0.05
	Trees ≥10 cm (no. stems/ha)	RN1	236.1 (58.6)	155.0 (31.1)	0.04
	Treed canopy 2-10 m high (%)	RN1	18.1 (3.7)	11.8 (2.6)	0.06
	Conifers >10 high suppressed (%)	RN1	22.8 (6.7)	6.8 (2.4)	0.05
	Shrub/fern <0.5 m high (%)	RN2	4.8 (0.9)	4.6 (1.0)	0.06
	Shrub/fern ≥0.5 m high (%)	RN1	15.6 (5.4)	5.7 (1.5)	0.09

[a] Ranhab1 = RN1. Ranhab2 = RN2. [b] Tests for 1996 that included the central non-breeder UN 52 were not significant; therefore, our 1996 significant results are for tests that excluded UN 52.

higher densities of suppressed trees occurred within known territories compared to those territories placed randomly (Table 3). In addition, 1996 territories had greater percent coverage from the canopy of stems <10 m high, and from deciduous shrubs and ferns, than those territories placed randomly (Table 3). Lower percent coverage of aerial wood occurred within territories in both 1995 and 1996 compared to that in the randomly placed territories by year, and this is consistent with the lower coverage of woody debris pieces <2 cm for 1996 (Table 3). Territories in 1996, but not in 1995, were closer to the edge of the study block and closer to streams compared to randomly placed territories (Table 3).

DISCUSSION

Dispersed Retention, Streams, and Edge

Winter Wrens located their territories nearer to streams and seeps in the study block in 1996 (Table 3), and this finding is consistent with our findings for the young and mature forests (Waterhouse et al. 2002). The association of territories with streams was weaker in 1995, which was a dry, mild year[7], but stronger in 1996, which was a wet and cool year[8]. Winter Wrens, like other bird species (Gray 1993), may improve their survival by shifting their foraging activities to best exploit available resources. For example, the drier habitats near streams and seeps in 1995 may have had reduced density of arthropods, thus causing wrens to forage elsewhere. Waterhouse (1998) suggests that wrens in the mature forest in 1995 compen-

[7] From April 16 to May 31,1995: 8 days with rain, 41 mm of rain, and average temperature of 15.3°C.
[8] From April 16 to May 31, 1996: 30 days with rain, 150 mm of rain, and average temperature of 12.0°C.

sated for the drier stream-side habitat by including more pieces of large downed wood in their territories as alternative foraging sites, because downed wood can retain arthropods even as the duff and soil dries out (Harmon et al. 1986). However in the study block, the amount of downed wood in territories did not differ from that in the random placements. Instead, perhaps wrens foraged more along the edge between the dispersed retention area and the mature forest in 1995 because edge, particularly in drier conditions, can be a more productive source of arthropods (Mattson and Haack 1987; Kremsater and Bunnell 1999). In 1995 and 1996, the tendency of territories to be in the same locations but with shifted boundaries (Figures 2 and 3) may reflect the wrens' compromise between retaining productive edges in their territories while also foraging on abundant arthropods near stream-side habitats available during the wetter conditions of 1996.

The inter-annual shift in habitat use was also demonstrated strongly by nest location. In both years, nests were located relatively close to streams or seeps and this is also consistent with our findings for the young and mature forests (Waterhouse et al. 2002). But in the drier year (1995), nests were located within the dispersed retention area as opposed to the mature forest. Ambient temperature affects the metabolic rates of birds, and Winter Wrens require more energy during cool weather (Armstrong 1956). We propose the warmer weather in 1995 may have reduced the wrens' energy requirements thus improving the suitability of the open, exposed dispersed retention area and its edge for nesting habitat. Nests within the dispersed retention area, but close to the edge of the mature forest, would still receive some shade and shelter from the forest canopy. But in wet years, the wrens' energy requirements at these more exposed nests could be greater, thus locations within closed canopy forest habitat would be preferred. In both years, foraging or nesting (e.g., availability of nest substrates or thermoregulation) advantages for the Winter Wren might be associated with streams and seeps whether these habitats are used in a dispersed retention area or closed forest. Hence, Winter Wrens may select for streams and seeps to help ensure they place themselves in higher quality habitat at the stand level (Waterhouse et al. 2002). Once their territories are anchored at these potentially higher quality locations, Winter Wrens could then shift the position of their nests and territorial foraging activity as availability of food, weather, or other factors vary annually.

Dispersed Retention, Canopy, and Edge

The inconsistent between-year results from the randomization tests for habitat selection likely reflect the wrens' responses to annual changes in abundance and distribution of resources as well as intra-specific competition (Waterhouse 1998). Alternatively, these results might be an artefact of the sampling design and small sample size. Yet several aspects of habitat use were consistent between years. Lower amounts of aerial wood in the breeding territories compared to random sites suggest that Winter Wrens do not select for residue piles of small stems and branches that are by-products of harvesting, although they have been reported to use slash piles in clearcuts (Tobalske et. al. 1991). Thus the utility of the residue piles may change when there is no overstory canopy within the block from retained trees or from adjacent unharvested forest. The presence of fewer large trees and snags within territories was also consistent between years, and it likely reflects the influence of edge and amount of dispersed retention within territories. Winter Wrens in mature forest also selected habitats for nesting or singing with lower densities of trees and snags but with well-developed overstory canopies (Waterhouse et al. 2002). These sites likely originated from gaps created by streams or tree mortality, but with the overstory gap now closed following the expansion of the surrounding tree crowns (Waterhouse et al. 2002). Overstory canopy may provide better shelter from inclement weather, reduce exposure to predators, as well as produce moister and cooler microclimates more favourable for arthropods and nesting (Block and Brennan 1993; Duguay et al. 2000). Some structural characteristics of the 3–5 year post-harvest dispersed retention area are similar to those produced by gaps (e.g., open understory with fewer tree stems), but others differ (e.g., open compared to closed overstory canopy because it takes more than five years to attain substantial lateral branch growth). As well, the spatial scale at which suitable habitat occurs for Winter Wrens differs between forest and a dispersed retention area. The small pockets of open areas used by wrens occur as patches of preferred habitat within the larger-scale territory in young and mature stands, whereas an entire territory can occur within the dispersed retention area. These differences may reduce habitat quality of the dispersed retention area for the Winter Wren. Hence, the placement of territories along edges may allow Winter Wrens to access both open and closed habitats as they do in the fine-grained habitat mosaic of young and mature forests.

If adult wrens, like other birds (Hilden 1965), select for the most optimal breeding habitats, then the behaviour of wrens on the central territory further suggests that the quality of the dispersed retention area as Winter Wren habitat may, in some years, be sub-optimal without the presence of adjacent mature forest. The failure of the central territory holder to breed in 1996 and the absence of a territory in 1997[9] support this notion of low habitat quality during cooler wet years. The successful breeding of GPB in 1995 suggests a warmer year might potentially mask a reduction in habitat quality or actually improve habitat quality. However if GPB was a pre-harvest terri-

[9] From April 16 to May 31 1997: 24 days with rain, 131 mm of rain, and average temperature of 14.4°C.

tory holder from 1993, he may also have returned because of site tenacity, and his familiarity with the site may have influenced his success at breeding. Site tenacity, which is common among birds (Hilden 1965), occurs in Winter Wrens because some wrens in the adjacent mature forest maintained the same territories for at least three consecutive years (Waterhouse 1998). In this case, the quality of the dispersed retention area may have been lower in all years, and our observation of breeding in the dispersed retention area during 1995 may have occurred because of site tenacity. Yet, in 1995, the locations of nests in the dispersed retention area compared to the mature forest suggests some interaction between the weather and nest location.

Application to Forest Management

In south coastal British Columbia, the Winter Wren is most abundant in mature and older forests, but is generally absent in young clearcuts (<5 years) (Savard et al. in press). The density of wrens in the dispersed retention study block was within the range reported for adjacent mature forests (Waterhouse 1998). Our results show differences in habitat use among years, likely because of reduced structure in the dispersed retention area and also potentially from increased availability and distribution of arthropods on edges. Furthermore, it appears that this dispersed retention area was sub-optimal habitat for breeding males in cool wet years or following loss of the pre-harvest territory holder. Yet a dispersed retention area may have value by supporting subordinate males until they can successfully breed (Hilden 1965). However, Winter Wrens can occupy a dispersed retention area and successfully breed if they also have access to mature forest. Given our findings for the study block and from Waterhouse (1998), we expect that Winter Wrens, in the long-term, will increasingly exploit dispersed retention stands as the overstory canopy closes with expanding tree crowns, and as the influence of edge abates with stand development. But, if the forest-management objective is to manage for Winter Wrens, then habitat quality in the long-term may need to be enhanced by removing some trees to re-open stands if such gaps do not develop on their own. In addition, providing Winter Wrens with substrates for nesting and feeding throughout the development and growth of the dispersed retention stand would need to be addressed during planning. In silvicultural treatments where there are greater amounts of retention (i.e., >53 stems/ha), habitat quality for Winter Wrens may differ from that in this study.

Winter Wrens require suitable nest substrates for building their nests, and these include logs (mostly >30 cm diameter at least at one end), root wads, and snags. In the mature forest, logs used for nesting were on average 50 cm diameter (SE 4 cm, n=36) (Waterhouse 1998). A range of snags was used depending on the type of nests: for nests located behind bark, the snags averaged 29 cm dbh (SE 3 cm, n=11); and for nests located in crevices, the snags averaged 54 cm dbh (SE 8 cm, n=8). These structures need to be retained, with provisions to recruit new ones, and they need to be distributed throughout managed stands so that the wrens in each territory have access to them. Streams also have an overlying effect on wren distribution (Waterhouse et al. 2002), thus managers may need to consider retention and recruitment of some stream-side habitats and their associated structures to maintain habitat values for the wren in dispersed retention stands.

In general, retention harvesting systems are thought to mitigate effects of timber harvesting on bird communities (Annand and Thompson 1997; Duguay et al. 2000), and the magnitude of this mitigation may be directly related to the amount of retained structures (Norton and Hannon 1997; Steventon et al. 1998). Based on our findings, we think that the overall effect on wildlife will depend also on the size of the dispersed retention block and its juxtaposition to other forest types. For example, Winter Wrens were able to access mature forest because the retention area was small (i.e., 7.1 ha) and their use of this adjacent forest might have reduced the overall effect of harvesting on the population in the cutblock. Furthermore consideration needs to be given to whether trees should be aggregated or dispersed during retention. More wildlife species may benefit with aggregated retention because additional habitat characteristics associated with mature stands such as microclimate and late-seral understory vegetation can also be maintained (Hansen et al. 1995; Beese and Bryant 1999; Hartley 2002). Furthermore, aggregation may reduce windthrow hazard, particularly in stream-side or wet areas, as well as benefit those tree species which maximize growth under full sunlight (D'Anjou 2001a; D'Anjou 2001b; Hudson and D'Anjou 2001). In general, a combination of different stand-level harvesting systems are recommended for a landscape because different systems may benefit different species (Steventon et al. 1998; Chambers et al. 1999; Bunnell 2002).

CONCLUSIONS

From 1995 to 1997, on the south coast of British Columbia, we studied habitat use by Winter Wrens in a 7.1-ha dispersed retention area located within a 13.1 ha study block of mature forest (>120 years). Our research indicated that behaviour and habitat use of wrens in the dispersed retention area differed from that observed in young and mature forests, and that these differences were in response to changes in forest stand structure and to creation of edge adjacent to the mature forest. However, similar to Winter Wrens in young and mature forests, wrens in the dispersed retention area were influenced by streams and factors that vary annually, such as weather and food sources.

This pilot study and our findings in young and mature forests (Waterhouse et al. 2002), indicate Winter Wrens occupy structurally complex sites that contain downed wood, root wads, and snags. These structures are products of several ecological processes. Large-diameter snags occur because of the ecological process involving growth, decline, death, and decay of trees (Harmon et al. 1986). The small canopy gaps that contain logs and root wads occur because of factors that perpetuate this natural disturbance regime (Lertzman et al. 1996). The layered structural complexity at gaps in the stand and at streams and seeps occurs because of ecological processes that support the diversity of plant species and regenerating trees (Radeke 1988; Lertzman et al. 1996). The presence of Winter Wrens across a managed stand, in part, reveals that these ecological processes continue to operate in the managed stand, or that appropriate mature forest legacies have been retained. If these ecological processes continue to operate in the managed stand, new structures will be recruited and thus help maintain habitat for Winter Wrens over the long term. The structural features and ecological processes that support Winter Wrens also support other forest-dwelling organisms and thus contribute to the biodiversity in stands. Understanding how dispersed retention can change availability of structural features and ecological processes that provide habitat for a species can help managers design forest practices that can better provide habitat for wildlife.

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Appendix A: Mean and SE of Site Characteristics (n=47) and Habitat Attributes (n=48) of the Study Block

Variable	Mean	SE
Site characteristics		
Slope	15.6	1.7
Aspect	202.1	2.0
Habitat attributes		
Nearest water source (m)	47.2	4.9
Nearest forest edge (m)	42.9	4.0
Downed wood <2 cm (%)	7.3	0.8
Downed wood 2-7 cm (%)	5.2	0.6
Downed wood ≥7 cm (%)	8.3	0.5
Aerial wood (%)	1.9	0.4
Mosses (%)	4.8	0.6
Shrubs <0.5 m high (%)	4.0	0.6
Deciduous shrub/fern <0.5 m high (%)	4.7	0.7
Total vegetation <0.5 m high (%)	10.3	1.9
Shrubs ≥0.5 m high (%)	4.3	2.0
Ferns ≥0.5 m high [a] (%)	5.4	1.0
Deciduous shrub/fern ≥0.5 m high (%)	9.4	2.3
Coniferous main canopy (%)	43.4	6.4
Coniferous intermediate (%)	4.6	1.3
Coniferous suppressed (%)	12.8	3.1
Coniferous total >10 m high [a] (%)	47.9	6.3
Coniferous 2-10 m high (%)	13.1	2.1
Treed overstory canopy (%)	15.1	2.3
Treed understory canopy (%)	48.1	6.3
Trees <10 cm dbh, ≤10 m high (no. stems/ha)	766.7	87.6
Trees ≥10 cm dbh, ≤10 m high (no. stems/ha)	32.3	9.2
Trees ≥10 cm dbh, >10 m high (no. stems/ha)	185.4	29.5
Trees ≥10 cm dbh (no. stems/ha)	217.7	34.3
Trees 10-29 cm dbh (no. stems/ha)	101.0	20.4
Trees 30-49 cm dbh (no. stems/ha)	49.0	10.0
Trees 50-74 cm dbh (no. stems/ha)	46.9	11.3
Trees ≥75 cm dbh (no. stems/ha)	20.8	5.3
Trees ≥50 cm dbh (no. stems/ha)	67.7	12.9
Trees ≥30 cm dbh (no. stems/ha)	116.7	17.9
Soft snags <10 cm dbh, ≤10 m high (no. stems/ha)	10.4	4.5
Hard snags <10 cm dbh, ≤10 m high (no. stems/ha)	43.8	9.4
Snags <10 cm dbh, <10 m high (no. stems/ha)	54.2	11.5
Soft snags 10-29 cm dbh (no. stems/ha)	51.0	9.7
Hard snags 10-29 cm dbh (no. stems/ha)	191.7	22.3
Soft snags 30-49 cm dbh (no. stems/ha)	24.0	5.4
Hard snags 30-49 cm dbh (no. stems/ha)	89.6	14.7
Soft snags 50-74 cm dbh (no. stems/ha)	14.6	3.6
Hard snags 50-74 cm dbh (no. stems/ha)	53.1	8.6
Soft snags ≥75 cm dbh (no. stems/ha)	8.3	3.1
Hard snags ≥75 cm dbh (no. stems/ha)	11.5	4.3
Soft snags ≥10 cm dbh (no. stems/ha)	97.9	13.1
Hard snags ≥10 cm dbh (no. stems/ha)	345.8	39.1
Snags ≥10 cm dbh (no. stems/ha)	443.8	39.9
Snags ≤10 m (no. stems/ha)	425.0	41.3
Snags >10 m high (no. stems/ha)	18.8	6.3
Snags 10-29 cm dbh (no. stems/ha)	242.7	23.6
Snags 30-49 cm dbh (no. stems/ha)	113.5	15.5
Snags 50-74 cm dbh (no. stems/ha)	67.7	9.8
Snags ≥75 cm dbh (no. stems/ha)	19.8	5.1
Snags ≥50 cm dbh (no. stems/ha)	84.4	12.1
Snags ≥30 cm dbh (no. stems/ha)	197.9	23.0

[a] n = 47 instead of 48.